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Effects of spatial arrangement of visual stimulus on inverted self-motion perception induced by the foreground motion: examination of OKN-suppression hypothesis

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Abstract

Our previous study revealed that a slowly moving foreground, which is presented in front of a fast-moving orthogonal background, can induce self-motion perception in the same direction as its motion (inverted vection; Vis. Res. 40 (2000) 2915). The present study shows that inverted vection becomes stronger in the conditions where the foreground stimulus is presented in the central area of observer's visual field and the observer's eyes converge on the same depth plane. These stimulus conditions are consistent with the one where the foreground can induce observer's optokinetic nystagmus more effectively, and therefore, the results of this study support our hypothesis in that mis-registered eye-movement information caused by the suppression of optokinetic nystagmus induced by the foreground motion is a critical factor in perceiving inverted vection.

Keywords: Vection; Self-motion; Foreground; Eye-movement

1. Introduction

A visual stimulus that is presented on a large area of an observer's visual field and moves uniformly induces illusory motion perception of the observer's own body in the opposite direction to its motion. This perceptual phenomenon, which was called vection by Fischer and Kornmüller (1930), has been investigated as strong evidence for the effects of visual information on self-motion perception (see Warren, 1995, for a review). When we move in the natural environment, retinal images of externally stable objects move in the opposite direction to the self-motion. Thus vection reflects the natural relationship between real self-motion and retinal image motion of the external scene.

Psychophysical studies on vection have established that vection is induced by the most distant visual stimulus in the visual fields, and occurs in the direction opposite to such a background motion (e.g., Brandt, Wist, & Dichgans, 1975; Howard & Heckman, 1989; Ohmi & Howard, 1988; Ohmi, Howard, & Landolt, 1987). In natural circumstances, distant visual objects rarely move quickly, providing a reliable absolute frame of reference. Accordingly, the retinal image motion of the background most likely reflects the observer's self-motion in the opposite direction. Thus, it is a reasonable strategy for the perceptual system to depend on the background as a reliable frame of reference in perceiving self-motion. This might be the reason why vection is dominated by the background stimulus in most cases. Consequently, most vection studies have concentrated on analyses of the effects of the background stimulus, and ignored the effects of the foreground stimulus presented nearer to the observer.

Our previous investigation (Nakamura & Shimojo, 1999, 2000), however, revealed that the foreground stimulus could play an important role in perceiving self-motion. In particular, Nakamura and Shimojo (2000) indicated that, when foreground stimulus moves slowly in front of an orthogonally moving background stimulus, the observer perceives an oblique self-motion which is a result of vector summation between two motion components induced by the foreground and the

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background, and has a component whose direction is the same as that of the foreground. It is reasonable to assume that the moving pattern induces self-motion perception only in the direction parallel to, not orthogonal to, its own motion direction. If so, this finding suggests that a slowly moving foreground can induce self-motion perception in the same direction as its motion (although the orthogonal motion in the background provides a necessary condition). We named this newly discovered perceptual phenomenon as "inverted vection," because the relationship between the direction of perceived self-motion and that of visual inducer is inverted with regard to the conventional vection (self-motion perception in the opposite direction to inducer's motion). Inverted vection cannot be accounted for by the natural relationship between observer's self-motion and retinal image motion of the external background, which can only cause the conventional vection, as mentioned above. The perceptual or neural basis underlying two types of vection should be different, at least, partially.

Nakamura and Shimojo (2000) discussed two theoretical alternatives that can account for the inverted vection. One was based on relative motion between the foreground and the background inducers, and the other was based on mis-registered information about the observer's eye-movement. When the foreground and the background inducers move orthogonally, the foreground motion could bias perceived direction of the background motion opposite to its motion. The perceived direction of the background motion may be a result of vector summation of the original actual motion of the background and the induced component in it caused by the relative motion between the foreground and the background (Loomis & Nakayama, 1973; Post & Chaderjian, 1988). Note that the induced component is in the opposite direction to that of the foreground inducer. Such a biased motion of the background then would induce a self-motion perception with a component that is apparently in the same direction as the foreground motion (because it would be the opposite of the opposite). Thus the relative motion between the two inducers can be the critical factor generating inverted vection. However, one of our experiments revealed that inverted vection can also be induced by stimulus combination of a vertically moving foreground and a vertically striped background which moved horizontally (Nakamura & Shimojo, 2000). Vertical stripes have no luminance gradient along the direction in which the foreground random-dots were moving, so the vertically moving foreground dots cannot induce a vertical motion of the vertically striped background. In this combination of background and foreground, no biased motion of the background was induced, yet inverted vection was perceived. We thus concluded that the relative motion between two inducers cannot account for the inverted vection.

As an alternative account, we hypothesized that mis-registered information about the observer's eye-movement would contribute to inverted vection. Post and his colleagues (e.g., Post, 1986; Post & Leibowitz, 1985; Post, Shupert, & Leibowitz, 1984) suggested that observation of a translating pattern with stable fixation would evoke mis-registration of eye-movement information in the opposite direction to the visual motion, due to a suppression of optokinetic nystagmus (OKN), which could be induced if there were no fixation. The suppression of OKN by the fixation is equivalent to the cancellation of it by intentional pursuit in the opposite direction (which is not executed actually), and mis-registration of eye-movement would occur in accordance with this intention. We speculated as follows; in a situation where the inverted vection is induced, the foreground motion causes mis-registration of eye-movement information as if the eyes moved in the orbit in the opposite direction to the foreground motion because of the OKN-suppression. Meanwhile, it is known in the heading perception literature that observers utilize information about eye-movement in order to correctly perceive the direction of self-motion when they translate forward with their eyes rotating (e.g., Royden, Banks, & Crowell, 1992; Royden, Crowell, & Banks, 1994). Eye-movement information would shift the observer's perception of heading direction from focus of expansion of optic flow pattern in the opposite direction to the eye-movement. Likewise, in inverted vection, the eye-movement information mis-registered by the foreground motion may affect self-motion perception, and perceived direction of the self-motion originally induced by the background motion may be biased in the opposite direction to the mis-registered eye-movement, i.e., in the same direction as the foreground inducer (see Nakamura & Shimojo, 2000, for more detailed discussion). We call this "OKN-suppression" hypothesis. It should be noted that the role of the foreground motion on self-motion perception is only a modificational one that affects direction of self-motion which is originally induced by the background motion.

Although mis-registration of eye-movement is a possible candidate for causing inverted vection, there has been no experimental support for this hypothesis. In this study, we aimed to test the OKN-suppression hypothesis by measuring the magnitude of inverted vection under various stimulus conditions. If our hypothesis were correct, there would be a stronger inverted vection in a condition where the foreground can evoke OKN more effectively so that the magnitude of mis-registered eye-movement information becomes stronger. Many studies have revealed stimulus conditions where the observer's OKN is evoked more effectively. In particular, a moving inducer presented in a central area of observer's visual field can induce stronger OKN than the one presented in the periphery (e.g.,

Barnes & Hill, 1984; Howard & Ohmi, 1984; Van Die & Collewijn, 1982, 1986). Thus, an inverted vection would be more strongly induced with the central foreground than the peripheral foreground. This prediction is in stark contrast to the one based on the assumption that the inverted vection has a similar underlying mechanism as conventional vection. In this scenario, it would be expected that the peripheral foreground induce stronger inverted vection than the central foreground. It has been repeatedly shown that a moving stimulus presented peripherally induces much stronger conventional vection than the one presented centrally (e.g., Berthoz, Pavard, & Young, 1975; Brandt, Dichgans, & Koenig, 1973; Johanson, 1977).

In Experiments 1 and 2, we examined the effects of the stimulus eccentricity where the moving foreground is presented. In Experiment 3, we examined the effect of the depth distances between the foreground and observer's convergence—yet another stimulus factor that affects the gain of OKN. OKN is evoked most effectively in the condition where the inducer is presented on the depth plane of the observer's convergence (i.e., on the horopter), and is diminished in increments of the depth separation between the planes (e.g., Howard & Gonzalez, 1987; Howard & Simpson, 1989). Again, this is different from conventional vection that is induced most effectively by a more distal plane, regardless of the vergence (e.g., Brandt et al., 1975).

2. Experiment 1

2.1. Method

2.1.1. Stimulus and apparatus

Visual stimuli used in the experiment were two overlapping random-dot patterns set to move orthogonally with each other. The foreground stimulus had a binocularly crossed disparity of 36′ corresponding to the situation where it was 15 cm nearer than the screen. The background stimulus was given an uncrossed disparity of 27′ which would let the pattern be perceived 15 cm farther than the screen (our informal observations had confirmed that perception in each case was very close to the prediction from the disparity). A fixation cross, whose size was 1 deg in height and 1 deg in width, and whose luminance was 14.8 cd/m^2, was also presented in the center of the screen with zero-disparity. Each dot in the pattern had a luminance of 14.8 cd/m^2 and a size of 3.2 deg in diameter. Dot density was 0.02 dots/deg^2. Fig. 1 illustrates the stimulus schematically.

The area of a screen where the foreground stimulus was presented on was determined in accordance with the stimulus conditions described in the next section. Background stimulus was always presented on the entire area of the screen. The foreground stimulus moved horizontally from left to right at a constant speed of 5 deg/s, and the background stimulus moved vertically upward at 25 deg/s. Our previous experiments have revealed that these velocities are optimal for inducing inverted vection. [2]

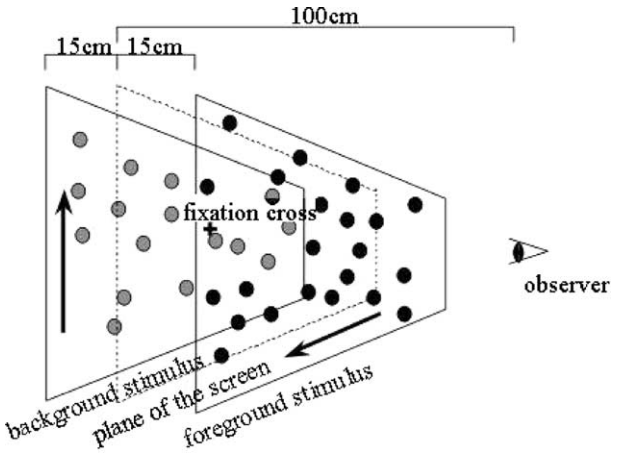

Fig. 1. Schematic illustration of the perceived layout of the stimulus used in Experiment 1. The foreground pattern was perceived to be 15 cm nearer and the background pattern was perceived to be 15 cm farther than the plane of the screen. The foreground pattern was set to move horizontally rightward at a speed of 5 deg/s and the background pattern moved upward at 25 deg/s. Arrows in the figure indicate motion directions of the stimulus patterns. The foreground pattern presented in central circular area (central condition), peripheral annular area (peripheral condition) or entire area of the screen (full-screen condition). Figure indicates the full-screen condition, as an example. A fixation cross was presented on the plane of the screen.

The stimuli were generated by a graphics workstation (SiliconGraphics IRIS320VGX) and projected to a screen 115 cm high and 200 cm wide by a 3D video projection system (Sony Tektronix 4190). 3D perception was accomplished by flickering orthogonal polarizing filters on the projector and by polarization goggles worn by subjects.

2.1.2. Procedure

Subjects were four adult volunteers (three males and one female, ages ranged from 24 to 33 years) with corrected-to-normal vision. All of the subjects had previous experiences of vection observations, but were naive to

[2] One may have a question whether subjects can correctly maintain their gaze on the stable fixation target in the stimulus situation employed here. I carried out post hoc experimental trials to address this issue using another three naïve observers. In these trials, same experimental procedure as the main experiment was replicated with monitoring observer's eye-movement by EOG (electro oculo graphy) method. The results indicated that, after an adequate training period (five trials or so), all observers can control their fixation correctly even in the condition where there were moving visual patterns, regardless of the stimulus condition, such as stimulus eccentricity where moving foreground is presented and the depth separation between the foreground stimulus and the fixation target.

the aim of the experiment. Subjects sat in a darkened room in an upright position in front of the screen, without a chin rest or any other head constraints, and observed the stimulus with their eyes fixated on the fixation cross at a viewing distance of 100 cm. Subjects wore goggles with orthogonally polarized filters for stereoscopic observations. The edges of the goggles limited the subjects' visual fields to 60 vertical deg and 90 horizontal deg, and they could not see anything other than the stimulus, such as edges of the screen, or the wall and the floor of the room. Stimulus presentation lasted for 120 s.

The procedure to measure the strength of inverted vection was the same as the one used in Nakamura and Shimojo (2000). While the orthogonally moving foreground and background stimuli together induce vection in an oblique direction, the subjects were instructed to attend only to the horizontal component, which is parallel to the foreground motion (our previous study indicates that the subjects can easily perform the task, and that the obtained data are reliable). If there were no foreground effects, observer's self-motion perception would be determined solely by the background motion, therefore induced only in the direction parallel to the background (orthogonal to the foreground), without any component parallel to the foreground motion. On the other hand, if the effect of the foreground is substantial, a significant self-motion component parallel to the foreground motion would be expected. Thus, we can assess the effect of the foreground by analyzing the self-motion component parallel to its motion.

As indices of the perceived strength of inverted vection, we measured the duration and the estimated magnitude of self-motion in the direction parallel to the foreground. Subjects had a button in each hand and were instructed to press the right button when they perceived rightward vection, and the left for leftward vection. They did not press any of the buttons when the self-motion appeared vertically without any horizontal component, as well as in the case where there was no perceived self-motion.

After the end of the stimulus presentation, subjects estimated perceived strength of the horizontal component of vection experienced during experimental trial. In order to establish the standard of the estimation, subjects underwent 10 training trials using the standard stimulus before all experimental trials. The standard stimulus consisted of a single random-dot pattern that was presented on the plane of the screen and had the same stimulus attributes as the background pattern used in the experimental trials. The standard stimulus moved from left to right at a speed of 50 deg/s. In the experimental trials, subjects estimated the strength of horizontal component of vection using a scale from 0 (no horizontal self-motion was perceived) to 100 (horizontal self-motion component was as strong as in the training trials), or beyond.

2.1.3. Stimulus condition

The area of the screen where the foreground stimulus was presented was varied as an independent variable, while the area of background stimulus was always presented on entire area of the screen. There were three different types of foreground stimulus, namely central, peripheral and full-screen. In the central and the peripheral foreground conditions, the foreground stimuli was presented to a central circular or a peripheral annular area, while the foreground was projected on the entire area of the screen in the full-screen condition. The radius of the central foreground and the inner radius of the peripheral foreground were 30 deg. The sizes of the outer edges of the peripheral foreground were 60 vertical deg and 90 horizontal deg. Consequently, the size of the foreground stimulus was 2826 deg^2 in the central, 2574 deg^2 in the peripheral and 5400 deg^2 in the full-screen foreground condition, respectively. Difference of the foreground sizes between the central and peripheral conditions was less than 5% of the screen-size and would be negligible.

Each experimental condition was repeated six times in a randomized order. Intervals between each trial were generous (3–5 min), and thus, it can be assumed that motion aftereffects caused by adaptation to the moving stimulus cannot affect following trials.

2.2. Results and discussion

Durations and estimated strengths were qualitatively consistent across the subjects. Thus, data were averaged across the subjects for each stimulus condition. In the data-analysis, a positive value was assigned to self-motion in the same direction as the rightward moving foreground (i.e., inverted vection), and a negative value was assigned to the opposite self-motion (i.e., conventional vection by the foreground motion). There were some trials in which two types of vection occurred alternately during stimulus presentation period. In such a trial, duration and estimated strength were measured individually first, and then, final indices were calculated by the summation of signed values for each direction.

In the full-screen and the central foreground conditions, all subject reported that self-motion perception was induced in the direction as the foreground motion (inverted vection was perceived), and conventional vection occasionally occurred only in a few exceptional trials. In the peripheral condition, subjects reported that no self-motion was perceived or only weak self-motion in either directions were induced. Fig. 2 shows averaged duration and estimated strength of horizontal self-motion parallel to the foreground motion under different foreground conditions. Positive values indicate self-motion perception in the same direction as the foreground motion (inverted vection). In the conditions of the central and the full-screen foreground, there were

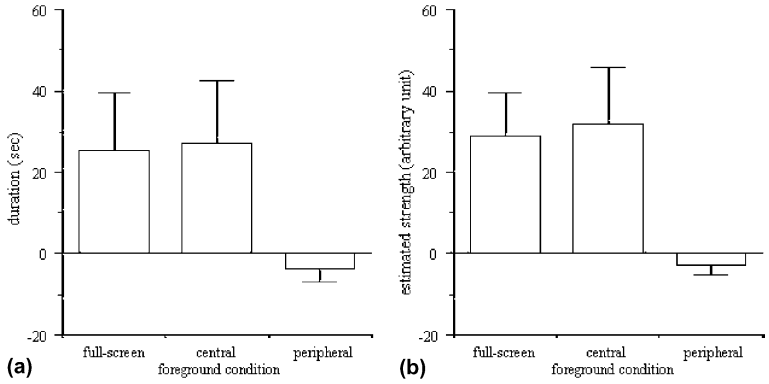

Fig. 2. Averaged duration (a) and estimated strength (b) of horizontal self-motion parallel to the foreground motion under each foreground condition. Positive values indicate self-motion in the same direction as the foreground stimulus (inverted vection), and negative values indicate self-motion in the opposite direction to the foreground (conventional vection induced by the foreground). Vertical bars indicate standard deviations.

much stronger inverted vections as indicated by longer durations and higher strength estimates. On the other hand, very little self-motion perception was induced in the peripheral foreground condition as indicated by shorter duration and lower strength estimate. The overall patterns of the results were highly consistent between two measures: Fig. 2(a) and (b). An analysis of variance indicated a significant main effect of the foreground types, both for duration and strength estimate ($F[2,6] = 14.43$, $p < 0.01$, $F[2,6] = 27.49$, $p < 0.01$, respectively).

The results of this experiment suggest that inverted vection is induced only when the central area of the observer's visual field is stimulated by the slowly moving foreground stimulus. It has been reported that conventional vection induced by the background motion was dominated by the peripheral area of observer's visual field (e.g., Brandt et al., 1973). The foveal dominance found in the current results distinguishes the inverted vection from the conventional type. [3]

It is also consistent with the known feature of OKN in that moving visual pattern presented in the central area of observer's visual field can evoke OKN more effectively than one presented in the peripheral area (e.g., Van Die & Collewijn, 1982). Thus, the result is consistent with our OKN-suppression hypothesis.

Furthermore, the present results revealed that there is no significant difference in inverted vection between the central and the full-screen foreground conditions, although the full-screen foreground was nearly twice as large as the central one in size. Conversely, the strength of conventional vection is known to increase monotonously as a function of the size of the moving pattern (Nakamura & Shimojo, 1998). Thus, the effects of stimulus-size, as well as the stimulus eccentricity, are different between the inverted and the conventional vections. These differences suggest that the mechanism responsible for inverted vection is different from that for conventional vection.

In Experiment 2, we further investigated the effects of the stimulus-size on inverted vection more precisely by using central stimuli with various sizes.

3. Experiment 2

3.1. Methods

Methods of this experiment were the same as Experiment 1, except for the stimulus conditions described below. Four adults volunteers participated in this experiment (three males and one female, ages ranged from 26 to 36 years). Two of them also took part in Experiment 1.

3.1.1. Stimulus condition

The foreground stimulus was presented on the central circular area. The radius of the foreground stimulus was manipulated as an independent variable in five steps, 10, 15, 20, 25, 30 deg. Accordingly, the foreground size was 316, 707, 1256, 1963, 2826 deg^2, respectively. In addition, there was also a control (full-screen) condition in which the foreground stimulus was presented on the entire area of the screen (stimulus-size: 5400 deg^2). The background stimulus was always presented on the entire area of the screen. Subjects underwent six trials for each condition in a randomized order.

[3] Some recent studies indicated that the central stimulus can induce conventional vection as strong as the one induced by the peripheral stimulus, if stimulus sizes are equal (e.g., Nakamura, 2001; Nakamura & Shimojo, 1998; Post, 1988). If so, there would be no effect of stimulus eccentricity on inverted vection based on the assumption that the effects of stimulus eccentricity are identical between inverted and conventional vections. The result of this experiment was also not compatible with this prediction.

3.2. Results and discussion

Averaged duration and estimated strength of self-motion parallel to the foreground motion were obtained with the same procedure as in Experiment 1. All subjects reported that self-motion was induced in the same direction as the foreground motion in almost all the trials. Fig. 3 indicates duration and estimated strength of inverted vection as a function of the foreground radius. The strength of inverted vection indicated by duration and estimation increased linearly with the size of the foreground stimulus, but the effect of the stimulus-size was saturated beyond the foreground radius of 20 deg. Analysis of variance indicated a significant main effect of the stimulus-size condition, both for the duration and the strength estimate ($F[5,15] = 3.65$, $p < 0.05$ and $F[5,15] = 5.26$, $p < 0.01$, respectively). Moreover, multiple comparison by Tukey's test revealed that the strength of inverted vection in the conditions of the foreground radius of 10 and 15 deg were significantly different from the one in the control condition where the foreground stimulus was presented on the entire area of the screen. There was no significant difference between the control condition and experimental conditions with the foreground radius larger than 20 deg, both for duration and estimation (duration: Mse = 37.77; estimation: Mse = 31.73 $\alpha = 0.05$ for all comparisons). This was the case even though the area of the entire-screen stimulus was nearly twice as large as that of the 30 deg radius condition.

The results of this experiment indicate that inverted vection is affected only by stimulation of the central area of the observer's visual field, and the peripheral portion of the visual field that is more eccentric than 20 deg has virtually no effect in inducing inverted vection. The results of this experiment, together with Experiment 1, are consistent with the previous finding that visual stimuli presented centrally can evoke stronger OKN than peripheral stimuli. For example, Van Die and Collewijn (1982) reported that, in the condition of peripheral stimulation with only 10 deg central occlusion (the rest of the visual field was stimulated by the moving pattern), the gain of OKN was decreased 45% as compared to the full-screen stimulus presentation, while central stimuli with 10 deg width can still evoke OKN with a gain decreased only 33%, relative to the full-screen. Unfortunately, we cannot compare the strength of inverted vection measured in the present study and the gain of OKN reported in these studies directly, because there were many differences in stimulus conditions. Further studies may be necessary to examine the causal relationship between OKN and inverted vection.

In the next experiment, we examined the effects of the depth distance between the foreground stimulus and the plane of observer's eye convergence, which should also affect the strength of OKN (e.g., Howard & Gonzalez, 1987), and therefore inverted vection, according to our OKN-suppression hypothesis.

4. Experiment 3

4.1. Methods

Methods used in this experiment were almost the same as in the previous experiments with the exception of the depth of the fixation cross. The four subjects who participated in Experiment 1 took part in this experiment.

Visual stimuli used in this experiment were the same as the full-screen condition of Experiment 1. Foreground and background patterns were presented on the entire area of the screen, and moved orthogonally at the velocities described in the stimulus section of Experiment 1. A fixation cross was presented at the center of the screen as in Experiment 1, but depth of the fixation cross was manipulated as an independent variable and had five different levels. Binocular disparity given to the

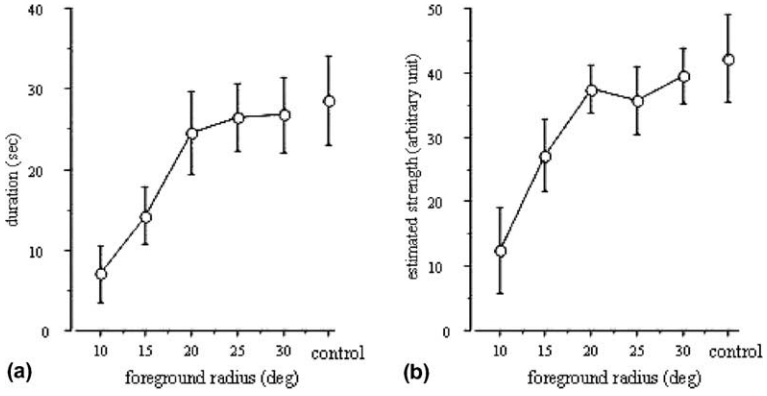

Fig. 3. Averaged duration (a) and estimated strength (b) of inverted vection as a function of the foreground size. Vertical bars indicate standard deviations.

fixation cross was −48′, −27′, 0′, +36′, +88′ (− means uncrossed and + means crossed disparities), and correspondent depth distance between fixation cross and the screen was −30, −15, 0, +15, +30 cm for each condition, respectively (negative values indicate that fixation cross was presented behind the screen, and positive values indicate that the fixation cross was presented in front of the screen). As in the previous experiments, the foreground pattern was presented 15 cm nearer than, and the background was 15 cm further than the screen. Thus, the fixation cross was presented on the same depth plane with the background pattern in the condition of −15 cm fixation, and with the foreground pattern in the condition of +15 cm fixation. A control condition without any fixation cross was also added. In the control condition, subjects were instructed to observe the visual pattern without intentional pursuit of any particular dot, and maintain their gaze around the center of the screen. Each experimental condition was repeated six times in a randomized order in the session.

4.2. Results and discussion

All subjects reported that only inverted vection, and no conventional vection, occurred as to the self-motion perception parallel to the foreground motion. Fig. 4 indicates averaged duration and estimated strength of inverted vection as a function of the depth distance of the fixation cross from the screen. The strength of inverted vection was varied systematically with the fixation depth. Inverted vection was strongest in the condition where the fixation cross was presented 15 cm nearer than the screen (+15 cm), as indicated by longest duration and highest strength estimate. It decreased when the depth varied from the +15 cm condition in either direction, near or far. An analysis of variance indicated a significant main effect of the fixation-depth condition, both for duration and strength estimate ($F[5, 15] = 9.69$, $p < 0.01$ and $F[5, 15] = 15.17$, $p < 0.01$, respectively). In the control condition without fixation cross, only a weak though significant inverted vection was perceived.

In the condition of +15 cm fixation condition where the strongest inverted vection was observed, the fixation cross was presented on the same depth plane as the foreground stimulus. It has been known that moving visual patterns presented on the depth plane where the observer fixated is most effective in inducing OKN, and the gain decreases with the increment of depth separation between the visual inducer and the observer's convergence (e.g., Howard & Gonzalez, 1987). The result of the present experiment again indicates that inverted vection becomes stronger in the stimulus condition where the foreground can potentially evoke eye-movement more effectively.

It is shown that conventional type of vection is affected by an additional stationary object and its depth relationship between a moving pattern. The conventional vection is suppressed by the stationary object presented behind the moving inducer, while it is facilitated when the stationary object is presented in front of the moving pattern (Brandt et al., 1973; Howard & Howard, 1994; Nakamura & Shimojo, 1999). Thus, if inverted vection shares perceptual mechanism with conventional vection, it is predicted that inverted vection is stronger when a stationary fixation cross is presented in front of the foreground stimulus, and becomes weaker with the fixation target presented behind the foreground. The result of this experiment is not consistent with this prediction, and suggests that the mechanisms responsible for the inverted and conventional types of vection are substantially different.

In the control condition where there was no fixation target, weak but significant inverted vection occurred.

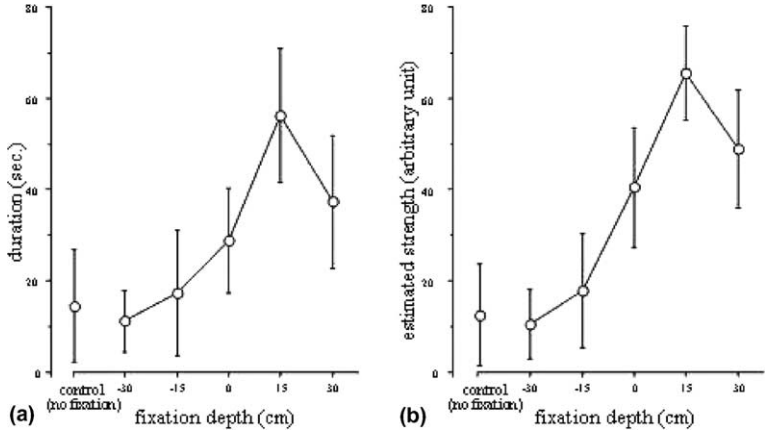

Fig. 4. Averaged duration (a) and estimated strength (b) of inverted vection as a function of depth distance of fixation cross from the plane of the screen. Positive values on abscissa indicate the conditions where fixation cross was presented in front of the screen, and vice versa for negative values. Vertical bars indicate standard deviations.

One may argue that this result contradicts the OKN-suppression hypothesis because there would be no OKN-suppression without overt fixation. This result might indicate that another factor, besides OKN-suppression, also contributes inverted vection. But there might still be a possibility that the result in the control condition can be attributed to the observer's eye-movement. In the control condition, there was no stable fixation target, but there was the background moving in orthogonal direction to the foreground. In such a condition, it can be assumed that the background which had no motion component in the direction parallel to the foreground might have tendency to inhibit observer's OKN to the direction as the foreground motion. This occasional tendency of gaze might have led to occasional or weak suppression of OKN, which in turn might have induced a weak though significant inverted vection. Perceptual mechanism responsible for inverted vection without overt fixation is unclear at this time, and further investigations must be needed to address this issue.

5. General discussion

A slowly moving foreground stimulus presented in front of a fast orthogonally moving background can induce self-motion perception in the same direction as the foreground motion. This perceptual phenomena named inverted vection was originally reported and investigated by the authors (Nakamura & Shimojo, 2000), and turned out to have quite different phenomenological features as compared with conventional vection. The results of experiments in the present paper revealed that inverted vection becomes stronger in conditions where the foreground stimulus is presented on the central area of the observer's visual field (Experiments 1 and 2) and on the depth plane of the observer's eye convergence (Experiment 3). Thus, strong inverted vection was induced in the conditions where the foreground stimulus was presented spatially close to the observer's locus of fixation, both in the observer's front-parallel plane and in the sagittal plane. These conditions were similar to the stimulus conditions where a moving visual pattern evokes observer's OKN most effectively, and is thus consistent with our OKN-suppression hypothesis about inverted vection.

In another experiment (Nakamura & Shimojo, 2003), we examined OKN-suppression hypothesis by directly manipulating the observer's gaze direction. The observer's sustained gaze-deviation affects inverted vection; the strength of inverted vection increases when observers deviate their gaze in the opposite direction to the foreground motion, while it decreases with gaze-deviation in the same direction as the foreground motion. Eye-movement information mis-registered in the perceptual system, which is supposed to be a primary factor for causing inverted vection, may be affected by the observer's gaze-deviation. Therefore, these results represented additional support for our hypothesis.

In a series of psychophysical studies on relative motion between visual objects, Gogel and his colleagues indicated that induced motion of visual objects were stronger in the condition where an induced target on which the observer fixates is located spatially adjacent to a moving inducer, whether they are presented coplanar or on different depth planes (adjacency principle; Gogel & Koslow, 1972; Gogel & MacCracken, 1979; Gogel & Tietz, 1976). These results are consistent with the effect of spatial adjacency between foreground inducer and observer's fixation on inverted vection in the present study.

It should be noted that there are other perceptual phenomena that are similar to inverted vection, in that an additional moving pattern biased the observer's self-motion perception in the same direction as the additional pattern. Duffy and Wurtz (1993) revealed that, when expanding and translating visual patterns are presented overlapping one on the other, perceived location of focus of expansion (FOE) in the expanding pattern shifts in the direction to which translating pattern moves. Royden and Hildreth (1996) also reported that perceived direction of self-motion (heading direction) is biased in the same direction as independently moving objects presented in front of expanding pattern which simulated retinal image motion of external scene during real self-motion (optic flow). These phenomena are affected by spatial layout of the additional moving inducer. Grigo and Lappe (1998) indicated that the shift of FOE was largest in the condition where translating pattern was presented on the same depth plane as the expanding pattern and decreased with increased depth distance between two patterns. Furthermore, Royden and Hildreth (1996) showed that an independently moving object could affect heading judgment only when the object was presented around FOE of the optic flow pattern. The spatial adjacency of moving object affects perceived location of FOE and heading direction in a similar manner to that affecting inverted vection. It is likely that similar mechanisms underlie these phenomena as well as inverted vection. Many experimental and theoretical studies have investigated perceptual mechanism responsible for the illusory shift of FOE. In these studies, mainly two factors have been discussed, namely observer's eye-movement (e.g., Duffy & Wurtz, 1993, 1995; Lappe & Rauschecker, 1995) and induced motion of visual objects (e.g., Grigo & Lappe, 1998; Meese, Smith, & Harris, 1995; Pack & Mingolla, 1998). However, as described in the introduction section, we confirmed that inverted vection can be induced in the situation where there is no relative motion between two visual inducers, using vertically striped background and

vertically moving foreground (Nakamura & Shimojo, 2000). Thus, induced motion caused by relative motion between visual patterns cannot be a primary factor in inducing inverted vection. Inverted vection may share the other factor with the illusory shift of FOE, that is, observer's eye-movement.

In conclusion, the results of the three experiments indicated that inverted vection is induced with greater strength in the condition where observer's OKN is potentially evoked more effectively and mis-registration of eye-movement information would be amplified. These results were consistent with our hypothesis that OKN-suppression leading to mis-registration of eye-movement is the critical factor for inverted vection.

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